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EFFECT OF TEMPERATURE ON THE HATCHING TIME OF EGGS OF FIVE *ECDYONURUS* SPP. (EPHEMEROPTERA) FROM AUSTRIAN STREAMS AND ENGLISH STREAMS, RIVERS AND LAKES

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SUMMARY

(1) Eggs of *Ecdyonurus picteti* from the Herrnalmbach and Seebach (Austria), *E. venosus* from Seebach and River Brathay (England), *E. dispar* from Windermere, Lake Ennerdale and River Lune (England), *E. insignis* from the River Eden (England) and *E. torrentis* from the River Lune, were fertilized artificially and kept at constant temperatures (range *c.* 3·5 °C to *c.* 20·5 °C) in the laboratory. The percentage of eggs that hatched at each temperature ranged from about 0·4% to 67·0% and there was no evidence that temperature was responsible for variations in hatching success.

(2) Hatching time (days after fertilization for 10, 50 and 90% of the eggs to hatch) decreased with increasing temperature and the relationship between the two variables within the temperature range 3·5–20·5 °C was well described by a power law, for all species except *E. dispar* from the River Lune. Therefore the effects of water temperature on the hatching time of *E. dispar* are very different to those on the other *Ecdyonurus* spp. There are inter- and sometimes intraspecific differences in the time taken for egg development of *Ecdyonurus* spp.

(3) The length of the period in which eggs were actually hatching was remarkably short for all species with no evidence for delayed hatching, except for *E. dispar* from the River Lune.

(4) A small number of field experiments were also performed in order to test the adequacy of the estimated values for the hatching time at different temperatures in the laboratory. There was a good agreement between the estimates and the actual hatching time in the field. Therefore the regression equations obtained from the laboratory experiments are probably applicable to eggs in the field, and both the number of days required for the eggs to hatch and the length of the hatching period can be estimated for all water temperatures from about 3·5 to about 20·5 °C.

INTRODUCTION

The mayflies, *Ecdyonurus dispar* (Curt.), *E. insignis* (Etn.), *E. torrentis* Kimm. and *E. venosus* (Fabr.) are widespread and abundant European species which occur in both continental Europe and Britain. A fifth species, *E. picteti* Meyer-Dür, is restricted to the Alps and Carpathians (Illies 1978), and its larvae are found in cold, stony streams.

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Larvae of the other four species occur on stones in streams and rivers whilst larvae of *E. dispar* are also found on the stony shores of large lakes (Macan 1970a; Kimmins 1972; Illies 1978). The life cycles of *Ecdyonurus* spp. have been frequently described (e.g. Rawlinson 1939; Pleskot 1951; Harker 1952; Macan 1957a; Elliott 1967; Landa 1968; Macan & Maudsley 1968; Thibault 1971; Sowa 1975) and some workers have found that the development pattern and the flight period can be markedly different for the same species in different biotopes and even in one biotope from year to year, e.g. adults of *E. picteti* are found from April to June in the Seebach, a mountain stream in Austria, but they are on the wing in September and October in a little stream at a higher altitude in the same mountains (Pleskot 1951). Some other workers have found that the flight periods of the different species in the same biotope may follow a definite pattern, e.g. adults of *E. torrentis* appear first followed by *E. insignis* and *E. dispar* (Landa 1962). From these field studies, some authors have suggested that these variations in the life cycle or this succession of species may be due to different patterns of egg development or larval growth, e.g. it is suggested that the eggs of *E. torrentis* hatch about one month after oviposition, while those of *E. dispar* and *E. insignis* do not hatch until the following year (Landa 1968; Sowa 1975).

Detailed information on egg development in Ephemeroptera is limited to *Baetis* spp. (Bohle 1969; Elliott 1972; Benech 1972), *Ephemerella ignita* (Poda) (Bohle 1972; Elliott 1978) and *Tricorythodes minutus* Traver (Newell & Minshall 1978). The aim of the present study was to study the hatching of *Ecdyonurus* spp. by rearing eggs from different populations and different biotopes in streams near Lunz (Austria), and streams, rivers and lakes near Windermere (England). The experiments were chiefly performed in the laboratory but a small number of field experiments were also performed to discover if the laboratory results were applicable to *Ecdyonurus* spp. in the field.

MATERIALS AND METHODS

Although adult females of *Ecdyonurus* spp. cannot be identified to species, the mature larvae of the English species and the sub-imagines of the English and Austrian species can be identified to this level. Therefore eggs of *Ecdyonurus* spp. were obtained from adult females which had been reared from mature larvae by methods which have already been described in detail by Humpesch (1971, 1979b). Eggs of *Ecdyonurus* spp. were also obtained from females that oviposited in the Seebach near Kazim (Austria) and the River Lune near Kirkby Lonsdale (England). Mature larvae of all species were collected from stones near the banks. *Ecdyonurus picteti* was obtained from the Herrnalmbach and Seebach (Austria), *E. venosus* from the Seebach and River Brathay (England), *E. dispar* from Windermere, Lake Ennerdale and River Lune (England), *E. insignis* from the River Eden (England) and *E. torrentis* from the River Lune (see appendix table). The Austrian streams are described in detail by Humpesch (1979a, b), the River Brathay is described by Macan (1957b), the River Lune by Macan (1976), Windermere and Lake Ennerdale by Macan (1970b).

Laboratory experiments

The eggs were fertilized artificially. As the method has been described in detail by Einsele (1958) for fertilization of pike eggs, only a brief account is given here. The abdomen of the female was crushed with two fingers and the expelled egg-mass was then transferred to a 10 × 1 cm dry, transparent plastic, Petri-dish by a preparation needle or forceps. Then the tip of the abdomen of the male was crushed, and the sperm was transferred to and mixed with the egg-mass with a preparation needle. The whole process of fertilization took about 2–3 min. After fertilization, the dish was half filled with water, which was subsequently changed at regular intervals, usually once a week throughout the whole experimental period. There was no forced aeration in the dishes.

The laboratory experiments were performed in cooled incubators or climate cabinets under different constant-temperature conditions and photoperiods (using artificial light). The water temperature was measured irregularly during the day and night over the whole experimental period in order to ascertain the most accurate mean temperature. In addition, a maximum and minimum thermometer was placed near the dishes in each climate room over the whole experimental period and was read under water in order to ascertain the range of the water temperature. The maximum light intensity at the surface of the dishes in each climate room was about 90 lux. For experiments in darkness, there was light only during the brief period of inspection. The eggs from one female were placed in one climate room, or divided into batches, each of which was placed in a different climate room. The eggs were counted under a binocular microscope.

Eggs kept at temperatures above 10 °C were examined daily whilst those kept below 10 °C were examined at intervals of 3 days or 4 weeks. When hatching commenced, the newly-hatched larvae were removed and counted. When hatching had apparently ceased, the dishes were examined for a further period of about 4 weeks for experiments at temperatures above 10 °C and up to 12 weeks for those below 10 °C. Eggs hatched in nearly all laboratory experiments with *E. dispar*. *E. insignis*, *E. picteti* from Seebach, *E. torrentis* and *E. venosus* from River Brathay. For *E. venosus* from Seebach and *E. picteti* from Herrnalmbach, eggs hatched in forty-four of 104 experiments and fifteen of forty-five experiments respectively. (Details of the month in which the eggs were fertilized, the water temperature, photoperiod, number of eggs used and percentage that hatched in each experiment, and the hatching period are given in the Appendix).

Field experiments

For experiments in the field, the fertilized eggs were enclosed inside bags made of nylon sifting cloth (mesh-size 0·01 mm). The bags were enclosed inside a cage of wire-netting (mesh-size 0·4 mm) for experiments in the Seebach, and in perforated plastic boxes for those in Windermere. The bags were washed in Petri-dishes every 2 days for the experiments in the Seebach and every 8 days for the experiments in Windermere. Newly-hatched larvae were removed and counted. When hatching had apparently ceased, the bags were regularly examined for at least 2 weeks. The water temperature was measured continuously with a temperature recorder in the Seebach, and with a thermometer three times a day (at 09.00, 14.00 and 23.00 hours) in Windermere. Nearly all the field experiments were successful for *E. dispar* in Windermere, but only one of four experiments with *E. picteti* in the Seebach and none of nine experiments with *E. venosus* in the Seebach were successful because the nets were washed away in spates.

RESULTS

Laboratory experiments

The number of eggs used at each temperature varied considerably in the range 83–4916 (see Appendix table). The percentage of eggs that hatched at each temperature ranged from about 0·4% to 67·0%, and there was no evidence that temperature was responsible for these variations in hatching success (see Appendix table).

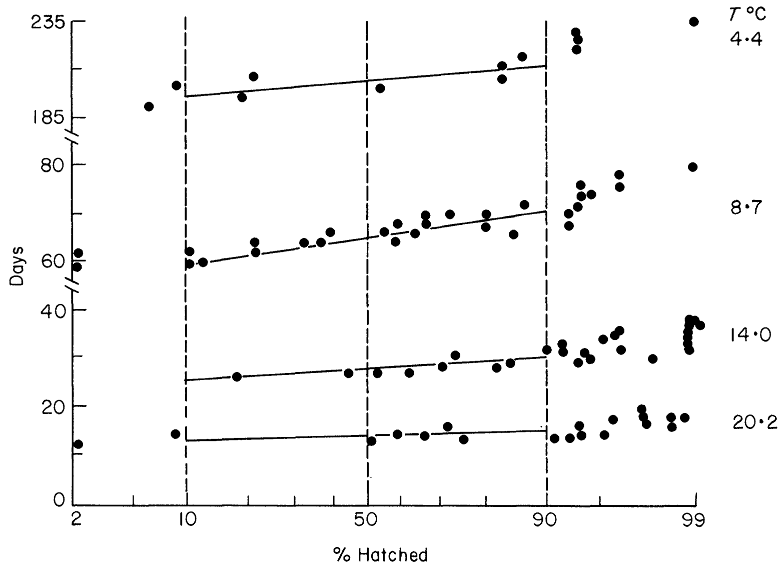

FIG. 1. Time required for eggs of *Ecdyonurus dispar* from Windermere to hatch at different temperatures (T °C) in the laboratory. Ordinate: number of days after fertilization. Abscissa (on probability scale): cumulative percentage of number of eggs hatched at each temperature.

As there was a large variation in the number of eggs hatching at each temperature, the counts of newly-hatched larvae were expressed as a cumulative percentage of the total number of eggs (= 100%) that hatched at each temperature. When these cumulative percentages were plotted against time (Y days after fertilization), they approximated a normal probability distribution in each experiment for all *Ecdyonurus* spp. (e.g. Fig. 1), except for *E. dispar* from the River Lune. Therefore the subsequent analyses were suitable for all species except *E. dispar* from the River Lune. As there were very few results for days required for hatching below 10% of the total number of eggs hatched, and the agreement with the normal distribution was poor above 90% of the total number of eggs hatched, it was not possible to estimate accurately the hatching time near the start and finish of the hatching period. Therefore the times at which 10, 50 and 90% of the eggs had hatched were used in all subsequent analyses (see for example Fig. 1).

The relationship between the time required (Y days after fertilization) for 10, 50 and 90% of the eggs to hatch and water temperature (T °C) over the temperature range of about 3·5 to 20·5 °C was found to be curvilinear on an arithmetic scale and linear on a logarithmic scale for all *Ecdyonurus* spp. (e.g. Fig. 2(a), (b)), except *E. dispar* from the River Lune. Therefore the relationship between hatching time (Y days) and water temperature (T °C) is given by the regression equation:

$$Y = aT^{-b} \tag{1a}$$

or in logarithmic form

$$\log_e Y = \log_e a - b \log_e T \tag{1b}$$

where a and b are constants. All regressions were a good fit to the data and the F-values from the variance ratio were highly significant ($P < 0{\cdot}001$). The proportion (r^2) of the variance of Y due to the regression of Y on T was always $\geqslant 0{\cdot}97$, and therefore at least

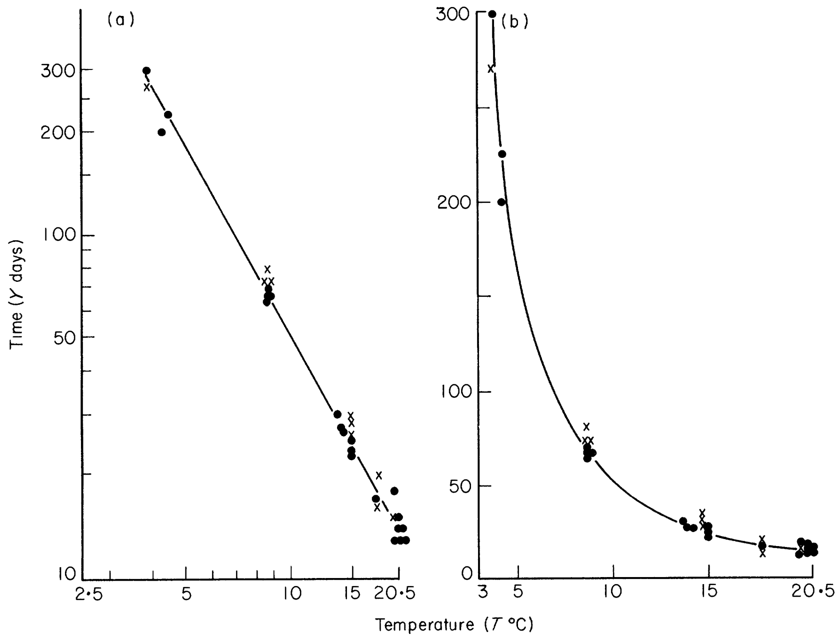

FIG. 2. Relationship between the time required (*Y* days) for 50% of the eggs to hatch and water temperature (*T* °C) in the laboratory, using pooled data for *Ecdyonurus dispar* from Windermere (●) and Lake Ennerdale (×): (a) On log/log scale with linear regression line. (b) On arithmetic scale with curvilinear regression line.

97% of the variability in the time required for hatching was accounted for by variations in temperature, which was clearly the major factor affecting the time required for hatching in the laboratory. Therefore the hatching time was apparently unaffected by variations in the time of the year when fertilization occurred or by variations in photoperiod (see Appendix table).

The values of the constants *a* and *b* from the regression equations for 10, 50 and 90% of eggs hatched differed between species and were often different for different populations of the same species (Table 1). This was not the case for *E. dispar*, and values of *a* and *b* for the Windermere population were not significantly different from those obtained for the Lake Ennerdale population. It was therefore possible to calculate one regression equation for eggs of *E. dispar* from both lakes by using the pooled results (see also Fig. 1(a), (b)). The value of *b* for eggs of *E. picteti* from the Seebach was not significantly different from that obtained for eggs of *E. picteti* from the Herrnalmbach, but their *a*-values were significantly different. Therefore the effect of temperature on rate of change in the hatching time was similar for both populations, but the rate of development at the same temperature was different. In *E. venosus*, the *a*- and *b*-values for eggs from the River Brathay were significantly different from those obtained for the eggs from the Seebach population. Therefore both the rate of change in hatching time and the development rate at the same temperature were different in the two populations. The values of *a* and/or *b* between the five species were always significantly different.

Estimates were made of the actual number of days required for 10, 50 and 90% of the eggs to hatch at 5, 10, 15 and 20 °C, and the *Ecdyonurus* spp. were ranked in order of decreasing hatching time at 5 °C (Table 2). In terms of days, differences between the

TABLE 1. Regression equations for the relationship between the time required for hatching of *Ecdyonurus* spp. and water temperature in the laboratory; showing the location where the mature larvae were found, the temperature range (T °C) at which the eggs were kept, the total number of experiments (n), the constants a and b from the regression equations for 10, 50 and 90% of eggs hatched (the coefficient of determination (r^2) was $\geqslant$0·97 for all regression equations which were all highly significant ($P < 0{\cdot}001$))

Species	Locality (country)	T °C	n	a ×÷ 95% C.L. 10%	a ×÷ 95% C.L. 50%	a ×÷ 95% C.L. 90%	b ± 95% C.L. 10%	b ± 95% C.L. 50%	b ± 95% C.L. 90%
E. dispar	Windermere (England)	3·9–20·3	23	2832·21 ×÷ 1·15	3241·69 ×÷ 1·19	3736·80 ×÷ 1·26	1·77 ± 0·05	1·81 ± 0·07	1·83 ± 0·09
	Ennerdale (England)	3·9–19·9	12	3145·21 ×÷ 1·49	3218·42 ×÷ 1·33	3844·29 ×÷ 1·29	1·78 ± 0·16	1·76 ± 0·12	1·82 ± 0·11
	pooled data	3·9–20·3	35	2998·56 ×÷ 1·18	3290·98 ×÷ 1·16	3804·82 ×÷ 1·18	1·79 ± 0·06	1·80 ± 0·06	1·83 ± 0·07
E. insignis	R. Eden (England)	8·7–19·9	12	7508·81 ×÷ 1·10	7881·28 ×÷ 1·20	8216·34 ×÷ 1·37	2·21 ± 0·04	2·22 ± 0·07	2·18 ± 0·12
E. picteti	Herrnalmbach (Austria)	3·5–17·3	15	1529·50 ×÷ 1·23	1654·74 ×÷ 1·23	1961·27 ×± 1·26	1·45 ± 0·09	1·47 ± 0·09	1·51 ± 0·10
	Seebach (Austria)	3·5–20·4	31	1145·77 ×÷ 1·12	1227·20 ×÷ 1·14	1212·83 ×÷ 1·15	1·46 ± 0·05	1·47 ± 0·06	1·44 ± 0·06
E. torrentis	R. Lune (England)	3·9–19·6	21	2541·83 ×÷ 1·26	2610·13 ×÷ 1·31	3734·70 ×÷ 1·42	1·83 ± 0·09	1·82 ± 0·11	1·93 ± 0·14
E. venosus	R. Brathay (England)	3·9–19·9	18	2528·41 ×÷ 1·21	3516·03 ×÷ 1·17	3906·42 ×÷ 1·18	1·79 ± 0·08	1·90 ± 0·06	1·91 ± 0·07
	Seebach (Austria)	3·6–20·6	44	2318·96 ×÷ 1·15	2592·96 ×÷ 1·16	2719·95 ×÷ 1·24	1·65 ± 0·06	1·68 ± 0·06	1·65 ± 0·09

TABLE 2. Estimates of the number of days (with 95% C.L.) required for 10, 50 and 90% of the eggs to hatch at 5, 10, 15 and 20 °C

% Hatched		10%				50%				90%			
T °C		5 °C	10 °C	15 °C	20 °C	5 °C	10 °C	15 °C	20 °C	5 °C	10 °C	15 °C	20 °C
E. dispar	Windermere, Ennerdale (pooled data)	169 ×÷ 1·07	49 ×÷ 1·03	24 ×÷ 1·03	14 ×÷ 1·04	180 ×÷ 1·06	52 ×÷ 1·03	25 ×÷ 1·04	15 ×÷ 1·05	201 ×÷ 1·07	57 ×÷ 1·04	27 ×÷ 1·05	16 ×÷ 1·06
E. venosus	Seebach	164 ×÷ 1·06	52 ×÷ 1·03	27 ×÷ 1·03	17 ×÷ 1·04	175 ×÷ 1·06	55 ×÷ 1·03	28 ×÷ 1·03	17 ×÷ 1·05	191 ×÷ 1·09	61 ×÷ 1·05	31 ×÷ 1·05	20 ×÷ 1·07
E. picteti	Herrnalmbach	148 ×÷ 1·11	54 ×÷ 1·06	30 ×÷ 1·07	—	155 ×÷ 1·08	56 ×÷ 1·06	31 ×÷ 1·07	—	172 ×÷ 1·09	61 +÷ 1·06	33 ×÷ 1·08	—
E. venosus	R. Brathay	142 ×÷ 1·08	41 ×÷ 1·05	20 ×÷ 1·06	12 ×÷ 1·07	166 ×÷ 1·06	45 ×÷ 1·04	21 ×÷ 1·05	12 ×÷ 1·06	181 ×÷ 1·07	48 ×÷ 1·04	22 ×÷ 1·05	13 ×÷ 1·06
E. torrentis	R. Lune	133 ×÷ 1·10	37 ×÷ 1·05	18 ×÷ 1·05	11 ×÷ 1·07	138 ×÷ 1·11	39 ×÷ 1·06	19 ×÷ 1·06	11 ×÷ 1·08	168 ×÷ 1·15	44 ×÷ 1·08	20 ×÷ 1·08	12 ×÷ 1·11
E. picteti	Seebach	109 ×÷ 1·04	40 ×÷ 1·03	22 ×÷ 1·04	14 ×÷ 1·05	115 ×÷ 1·05	41 ×÷ 1·03	23 ×÷ 1·04	15 ×÷ 1·05	120 ×÷ 1·05	44 +÷ 1·03	25 ×÷ 1·04	16 ÷÷ 1·06
E. insignis	R. Eden	—	46 ×÷ 1·02	19 ×÷ 1·01	10 ×÷ 1·02	—	48 ×÷ 1·03	20 ×÷ 1·02	10 ×÷ 1·04	—	54 ×÷ 1·06	22 ×÷ 1·04	12 ×÷ 1·06

TABLE 3. Regression equations for the relationship between the length of the hatching period (10–90% of eggs hatched) and water temperature in the laboratory; showing the location where the mature larvae were found, the total number of experiments (n), the constants a and b from the regression equations, the coefficient of determination (r^2) and the estimated values (days with 95% C.L.) for 3·5, 5, 6, 10, 15 and 20 °C (all regression equations were highly significant ($P < 0·001$))

Species	Locality	n	$a \overset{\times}{\div}$ 95% C.L.	$b \pm$ 95% C.L.	r^2	3·5 °C	5 °C	6 °C	10 °C	15 °C	20 °C
E. dispar	Windermere, Ennerdale (England) (pooled data)	35	923·46 $\overset{\times}{\div}$ 2·34	2·19 ± 0·35	0·83	59 $\overset{\times}{\div}$ 1·56	27 $\overset{\times}{\div}$ 1·40	18 $\overset{\times}{\div}$ 1·34	6 $\overset{\times}{\div}$ 1·24	2 $\overset{\times}{\div}$ 1·27	1 $\overset{\times}{\div}$ 1·35
E. insignis	R. Eden (England)	12	1196·92 $\overset{\times}{\div}$ 5·26	2·19 ± 0·63	0·86	—	—	—	8 $\overset{\times}{\div}$ 1·34	3 $\overset{\times}{\div}$ 1·25	2 $\overset{\times}{\div}$ 1·38
E. picteti	Herrnalmbach (Austria)	15	457·66 $\overset{\times}{\div}$ 3·51	1·83 ± 0·55	0·80	46 $\overset{\times}{\div}$ 1·85	24 $\overset{\times}{\div}$ 1·59	17 $\overset{\times}{\div}$ 1·49	7 $\overset{\times}{\div}$ 1·40	3 $\overset{\times}{\div}$ 1·54	—
	Seebach (Austria)	31	47·83 $\overset{\times}{\div}$ 3·07	1·11 ± 0·49	0·43	12 $\overset{\times}{\div}$ 1·73	8 $\overset{\times}{\div}$ 1·50	7 $\overset{\times}{\div}$ 1·40	4 $\overset{\times}{\div}$ 1·30	2 $\overset{\times}{\div}$ 1·42	2 $\overset{\times}{\div}$ 1·58
E. torrentis	R. Lune (England)	21	961·20 $\overset{\times}{\div}$ 5·42	2·25 ± 0·67	0·72	58 $\overset{\times}{\div}$ 2·44	26 $\overset{\times}{\div}$ 1·97	17 $\overset{\times}{\div}$ 1·78	5 $\overset{\times}{\pm}$ 1·45	2 $\overset{\times}{\div}$ 1·47	1 $\overset{\times}{\div}$ 1·63
E. venosus	R. Brathay (England)	15*	991·64 $\overset{\times}{\div}$ 3·19	2·24 ± 0·44	0·90	60 $\overset{\times}{\div}$ 1·86	27 $\overset{\times}{\div}$ 1·61	18 $\overset{\times}{\div}$ 1·49	6 $\overset{\times}{\div}$ 1·26	2 $\overset{\times}{\div}$ 1·22	1 $\overset{\times}{\div}$ 1·31
	Seebach (Austria)	44	394·54 $\overset{\times}{\div}$ 2·76	1·72 ± 0·41	0·63	46 $\overset{\times}{\div}$ 1·69	25 $\overset{\times}{\div}$ 1·49	18 $\div$ 1·40	8 $\overset{\times}{\div}$ 1·24	4 $\overset{\times}{\div}$ 1·27	2 $\overset{\times}{\div}$ 1·36

* This value of n is lower than that in Table 1 because there were no data for 10% times at 3·9 °C.

species at one temperature were remarkably high, the difference between the lowest and the highest value for 10% eggs hatched was about 8 weeks at 5, about 2 weeks at 10 and 15 and about 1 week at 20 °C. The period between fertilization and 10% eggs hatched varied from about 16 weeks at 5 °C to about 2 weeks at 20 °C. Table 2 also shows that as temperature decreases, the decrease in the number of days required for 10, 50 and 90% of the eggs to hatch is not the same for all species, e.g. although *E. picteti* (Seebach) starts to hatch earlier than *E. dispar* (lakes) at 5 °C, the two species start to hatch at the same time at 20 °C.

The length of the hatching period (Y days) for 10 to 90% of eggs hatched decreased with increasing temperature and the relationship between the two variables is given by Eqn (1). The values of the constants a and b are given in Table 3, which shows that the hatching period for *Ecdyonurus* spp. is remarkably short, varying from about four weeks at 5 °C to only 1 or 2 days at 20 °C.

The relationship between the time required for 50% of the eggs to hatch and water temperature for eggs of *E. dispar* from the River Lune is given in Fig. 3, which shows that these results did not agree with the relationship shown by all other *Ecdyonurus* spp. Therefore the effects of water temperature on the hatching time of *E. dispar* (River Lune) are very different to those on the other *Ecdyonurus* spp. The time required for 50% of the eggs to hatch for *E. dispar* (River Lune) was longer at 9·0, 14·5, *c.* 17·0 and 20 °C compared with the results for *E. dispar* from the lakes (Fig. 3). These obvious discrepancies indicate that further detailed studies are necessary on the egg development of *E. dispar* from rivers.

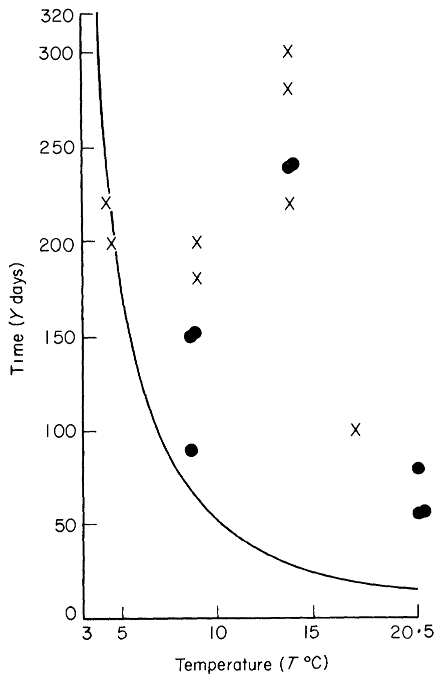

FIG. 3. Relationship between time required (Y days) for 50% of the eggs to hatch and water temperature (T °C) in the laboratory for *Ecdyonurus dispar* from the R. Lune (($\times$) eggs fertilized naturally; (●) eggs fertilized artificially; the curve is for the same relationship for *E. dispar* from Windermere and Ennerdale (see Fig. 2(b)).

Field experiments

Eggs were obtained from three females that were probably *E. venosus* and were ovipositing in Seebach on 14 August 1972 (17.00–18.30 hours). The eggs were placed in incubators at *c*. 10, *c*. 15 and *c*. 20 °C. Therefore it was possible to compare estimates derived from the laboratory experiments with artificially fertilized eggs and values obtained for eggs fertilized naturally. There was good agreement between the estimated values for 10 and 50% of the eggs to hatch from the artificially fertilized eggs and the actual hatching times for the eggs fertilized naturally, and only a slight disagreement for 90% of eggs to hatch (Table 4). Therefore the estimated values for the hatching time of eggs fertilized artificially are probably applicable to eggs fertilized naturally.

TABLE 4. The number of days required for 10, 50, 90% of the eggs to hatch in the laboratory, using (a) eggs from females of *E. venosus* (?) from Seebach fertilized naturally in August 1972; (b) eggs of *E. venosus* from the Seebach fertilized artificially in the laboratory (latter values were obtained from regression equations in Table 1 and are given as 95% C.L.)

T °C	Days for eggs fertilized					
	(a) naturally			(b) artificially		
	10%	50%	90%	10%	50%	90%
c. 10	52	53	56	50–54	53–57	58–64
c. 15	25	26	27	26–28	27–29	30–33
c. 20	—	15	19	16–18	16–18	19–21

The adequacy of the estimated values for the number of days required for 10, 50 and 90% of eggs to hatch at constant temperatures in the laboratory was also tested for fluctuating temperatures in both a stream and a lake. Although only one stream experiment with eggs of *E. picteti* (Seebach) and only six experiments with eggs of *E. dispar* (Windermere) were successful, there was good agreement between the results from the stream or the lake and the laboratory experiments (Table 5). There was only a slight disagreement in *E. dispar* (June) for 90% of eggs hatching in the field. Therefore the regression equations calculated from the results of all experiments with the five *Ecdyonurus* spp. are probably applicable to the hatching time in the field, and both the number of days required for 10, 50 and 90% of eggs to hatch and length of the hatching period (10–90% of eggs hatched) can be estimated for all water temperatures from about 3·5 to about 20·5 °C.

DISCUSSION

In this study, the percentage of eggs that hatched in each experiment was low compared with that obtained for other mayfly species, e.g. for *Baetis rhodani* (Pict.) (Bohle 1969; Elliott 1972; Benech 1972) or for *Ephemerella ignita* (Bohle 1972; Elliott 1978). These differences may be due to the technique of artificial fertilization and only a low percentage of eggs might be fertilized. While the percentage of eggs hatching varied considerably with temperature in *B. rhodani* (Bohle 1969; Elliott 1972; Benech 1972) and *E. ignita* (Bohle 1972; Elliott 1978), a similar effect of temperature was not observed for the *Ecdyonurus* spp.

There are no detailed studies on eggs of different species of the genus *Ecdyonurus*, but Percival & Whitehead (1928) noted that it took 15 days for eggs of *E. venosus* to hatch at *c*. 16 and Rawlinson (1939) found for the same species an egg development time of about

TABLE 5. The number of days (given as a range) required for 10, 50 and 90% of eggs hatching in the field and estimated values (given as 95% C.L.) obtained from regression equations in Table 1 (*n* is the number of experiments in the field and *T* °C is the mean ± S.E. and range of the water temperature in the field)

Species	Locality	Month	*n*	*T* °C Mean ± S.E.	*T* °C Range	Days required for hatching (a) in field 10%	(a) in field 50%	(a) in field 90%	(b) in laboratory 10%	(b) in laboratory 50%	(b) in laboratory 90%
E. picteti	Seebach	May	1	8·2±0·02	6·2–10·2	52–53	54–55	56–57	51–55	53–57	56–60
E. dispar	Windermere	June	3	16·5±0·33	13·8–21·7	—	18–25	26–33	19–21	20–22	22–24
		August	3	16·0±0·17	13·2–19·4	—	—	23–27	20–22	21–23	23–25

15–21 days in a temperature range of 14–17 °C. These hatching times are comparable to those obtained in the present study for eggs of *E. venosus* (River Brathay). A similar time for egg development was found for *E. forcipula* (Pict.) by Gros (1923) and Degrange (1960).

The present study has shown that, apart from eggs of *E. dispar* from the River Lune, the relationship between the time required for hatching and water temperature (in the range of *c.* 3·5 to *c.* 20·5 °C) for the eggs of five *Ecdyonurus* spp. is well described by a power law, and temperature has been shown to be the major factor for egg development in both the laboratory and the field. A similar relationship has been found for the egg development of *B. rhodani* (Elliott 1972; Benech 1972), *Tricorythodes minutus* (Newell & Minshall 1978) and for the stoneflies *Taeniopteryx nebulosa* (L.) (Brittain 1977) and *Nemurella picteti* Klp. (Brittain 1978), whilst Elliott (1978) has shown that for the eggs of *Ephemerella ignita* the relationship between the two variables, hatching time and water temperature, was well described by a hyperbola, and therefore the time taken for development could be expressed in units of degree-days above a threshold temperature.

There are interspecific and sometimes intraspecific differences in the time taken for egg development of *Ecdyonurus* spp. A comparison of the regression equations in the present study and those for other Ephemeroptera species (Elliott 1972, 1978; Benech 1972; Newell & Minshall 1978) shows that there are significant differences between species and that the time required for hatching can be described only by individual regression equations for each species. Bottrell (1975) explains some of the differences in the duration of the egg development of nine crustacean species from the River Thames by differences in egg size, the larger eggs taking longer to develop than smaller eggs at a given temperature, but there is a paucity of detailed work on egg size in different species of Ephemeroptera (see Degrange 1960).

There was agreement between the hatching times required for eggs of *E. dispar* from different lakes, and a similar agreement was found for eggs of *B. rhodani* populations from streams in the English Lake District (Elliott 1972), the Pyrenees (Benech 1972), and Germany (Bohle 1969). Therefore eggs of these species develop at similar rates in different localities and the regression equations appear to be valid for different populations.

The relationship between the time required for hatching and water temperature for eggs obtained throughout the flight period of *E. dispar* from the River Lune followed a pattern that differed markedly from that obtained from eggs of the lake populations (see Fig. 3). The simplest explanation for this difference is that eggs from the river population of *E. dispar* have a delayed hatching or a kind of dormancy whilst eggs from the lake populations do not. Khoo (1968) found that adults of lake and stream populations of the stonefly *Diura bicaudata* (L.) laid different types of egg. Adults from the Afon Hirnant, a stream in Northern Wales, laid only diapause eggs, whereas those from Lake Bala laid both diapause and non-diapause eggs, with a higher percentage of the latter. More detailed studies on the embryonic development of *E. dispar* from rivers are necessary before the obvious discrepancy in the hatching time between the lake- and the river populations can be explained. Further differences in the egg development times of the same species from different localities were found for *E. picteti* and *E. venosus*, which means that the regression equations for these species cannot be assumed to be applicable to other populations. The differences in the times for 90% of the eggs hatched are only about 1 week for both species at 15 and 20 °C, but they are much higher for *E. picteti* at 5 and 10 °C. The hatching times for the populations from the cooler environments, that is the Herrnalmbach for *E. picteti* and the Seebach for *E. venosus*, were always longer than those for the populations from the warmer environments. Intraspecific differences in the time required for hatching have been found in various animal groups, e.g. *Daphnia longispina* O. F. Müller (Munro & White 1975), *Salmo salar* L. (Peterson, Spinney & Sreedharan 1977). Some workers have suggested that these differences in the duration of egg development may be due to differences in egg size within the same species (Munro & White 1975). The latter relationship could not be analyzed for *E. picteti* and *E. venosus* because there is a lack of adequate data on their egg sizes.

The length of the period in which eggs were actually hatching was remarkably short for the *Ecdyonurus* spp. with no evidence for delayed hatching, except *E. dispar* from the River Lune. A similar short period and absence of delayed hatching was found for *B. rhodani* (Elliott 1972). A prolonged hatching period did occur for *E. dispar* from the River Lune and has been recorded for *Ephemerella ignita* (Bohle 1972; Elliott 1978) and *B. vernus* Curtis (Bohle 1969).

Information on hatching time is essential for the recognition and separation of cohorts of Ephemeroptera species in the field, and cohorts must be separated for accurate estimations of growth rates, mortality rates and production. The information presented in the present paper can be used to facilitate this separation. As a result of extensive field studies, Landa (1968) classified the life cycles of Central European Ephemeroptera into groups and types according to the number of generations per year. The number of generations per year was determined by observations on larval development in the field. He assumed that the eggs of some Ephemeroptera (e.g. *E. dispar*, *E. insignis*) passed through a diapause stage, because newly-hatched larvae or small larvae could not be found in the samples during the autumn and winter, long after the flight period. A similar interpretation has been made by several workers. The present study indicates that the classifications and assumptions of Landa (1968) are only partially correct, there is no evidence for an obligatory diapause in eggs of *E. insignis* (River Eden) and *E. dispar* (Windermere, Lake Ennerdale). Therefore, newly-hatched larvae or small larvae must be present in autumn and winter in the different localities. Very little is known about the occurrence, and biology of the newly-hatched larvae of *Ecdyonurus* spp. There is some information on the occurrence of young stages of Ephemeroptera and some workers have pointed out that most of them live deep in gravel beds (e.g. Macan 1958; Tilzer 1968) whereas most of the older larvae live nearer the surface. Therefore it may be difficult to find or catch the smaller larvae. This information is not available for individual species, because most of the young stages of Ephemeroptera cannot be identified. Therefore different patterns in the life cycle and succession of *Ecdyonurus* spp. can be partly explained by variations in their hatching times at different temperatures and in different localities, but further studies are necessary on larval growth and the factors affecting growth rates.

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APPENDIX

Source of eggs (species and locality where collected) and experimental conditions for hatching in *Ecdyonurus* spp., showing water temperature (T °C), photoperiod (LL = continuous light, DD = continuous darkness, L:D = ratio of hours of light: darkness, nLD = natural light/dark cycle in the field), number of experiments at each temperature (n), number of eggs at each temperature (mean number per experiment with range), percentage of eggs that hatched at each temperature (mean % per experiment with range), and the period over which the eggs hatched (days after fertilization).

Species	Locality	Month when fertilized	T °C Mean ± S.E.	T °C Range	Photoperiod	*n*	Number of eggs Mean	Number of eggs Range	Hatched eggs Mean %	Hatched eggs Range %	Hatching period (days)
E. dispar	Windermere (lake)	June 1978	3·9 ± 0·06	2·5–6·2	LL	3	497	320–668	21·83	8·13–41·42	270–320
		Oct. 1977	4·3 ± 0·07	3·6–6·6	DD	2	310	297–323	15·28	10·44–20·12	190–255
		Oct. 1977	8·7 ± 0·02	8·2–9·5	12L:12D	2	421	282–561	6·76	5·32–8·20	60–105
		June 1978	8·7 ± 0·02	7·9–9·0	12L:12D	2	382	353–412	17·38	3·88–30·88	60–95
		Aug. 1978	13·7 ± 0·03	13·3–14·1	12L:12D	1	563	—	40·32	—	28–39
		Oct. 1977	14·2 ± 0·04	13·6–15·0	14L:10D	2	407	322–492	15·99	14·29–17·68	26–45
		June 1978	15·0 ± 0·08	14·6–15·7	12L:12D	3	607	347–976	39·22	7·49–57·0	23–28
		June 1978	17·8 ± 0·08	17·1–18·5	LL	1	503	—	46·92	—	16–26
		June 1978	19·8 ± 0·01	17·4–21·1	LL	2	747	626–869	23·74	13·60–33·87	12–25
		July 1978	20·2 ± 0·03	19·4–20·7	LL	2	675	494–855	24·94	20·12–29·76	12–18
		Aug. 1978	20·2 ± 0·03	19·4–20·5	LL	1	1221	—	49·80	—	14–21
		July 1978	20·3 ± 0·04	19·5–20·7	DD	2	544	463–625	20·22	14·08–26·35	12–18
		June 1978	16·5 ± 0·33	13·8–21·7	nLD (Lake)	3	—	—	—	—	—
		Aug. 1978	16·0 ± 0·17	13·2–19·4	nLD (Lake)	3	—	—	—	—	—
	Ennerdale (lake)	June 1978	3·9 ± 0·06	2·5–6·2	LL	3	131	105–146	18·02	8·57–35·62	260–320
		June 1978	8·8 ± 0·03	7·9–9·5	12L:12D	3	118	80–184	32·26	18·75–39·13	66–88
		June 1978	14·9 ± 0·07	14·5–15·7	12L:12D	3	150	97–213	34·10	23·47–41·24	24–35
		June 1978	17·8 ± 0·08	17·3–18·5	LL	2	163	149–177	33·80	20·13–47·46	13–24
		June 1978	19·9 ± 0·10	17·4–21·1	LL	1	162	—	27·78	—	15–19
	R. Lune	Oct. 1977	4·4 ± 0·07	2·5–6·7	DD	2	297	260–334	4·92	3·29–6·54	160–292
		July 1978	8·7 ± 0·03	7·7–9·2	12L:12D	3	349	190–581	31·26	12·22–42·60	80–280
		Oct. 1977	8·9 ± 0·06	7·5–9·5	12L:12D	2	298	275–322	5·75	4·36–7·14	90–240
		Aug. 1978	13·8 ± 0·09	13·3–16·1	12L:12D	1	1061	—		—	54–*
		Oct. 1977	14·0 ± 0·04	12·6–16·5	12L:12D	3	327	248–484	8·19	2·02–15·70	60–364
		July 1978	14·1 ± 0·06	13·3–16·1	12L:12D	1	390	—		—	35–*
		Oct. 1977	17·4 ± 0·06	15·6–19·1	LL	1	411	—	3·16	—	24–134
		July 1978	20·1 ± 0·03	18·6–21·0	LL	3	690	193–1652	11·83	3·11–23·06	18–112
E. insignis	R. Eden	June 1978	8·7 ± 0·02	7·9–9·0	12L:12D	4	488	286–1003	8·50	4·82–15·81	60–80
		June 1978	14·5 ± 0·03	14·2–15·2	12L:12D	4	732	338–1123	11·24	9·63–12·10	20–30
		June 1978	19·9 ± 0·08	19·2–21·1	LL	4	476	304–793	12·68	9·22–16·78	10–15

* These experiments were finished in June 1979, when some eggs were still developing.

(continued)

Species	Locality	Month when fertilized	T °C Mean ± S.E.	Range	Photoperiod	n	Number of eggs Mean	Range	Hatched eggs Mean %	Range %	Hatching period (days)
E. picteti	Herrnalmbach (stream)	Aug. 1976	3·5 ± 0·02	2·6–4·1	10L:14D	1	3547	—	1·07	—	190–255
		Sept. 1977	3·9 ± 0·05	2·5–5·2	10L:14D	1	590	—	15·25	—	190–285
		Sept. 1977	4·4 ± 0·03	3·9–4·8	10L:14D	3	234	172–325	12·67	8·14–19·69	190–250
		Sept. 1977	8·2 ± 0·02	7·4–10·1	LL	1	732	—	1·23	—	70–79
		Sept. 1977	10·1 ± 0·04	9·8–10·5	10L:14D	1	228	—	7·46	—	52–57
		Sept. 1977	10·2 ± 0·03	9·9–10·7	10L:14D	1	1497	—	9·75	—	48–64
		Sept. 1977	13·2 ± 0·03	12·6–13·8	10L:14D	1	163	—	12·88	—	35–48
		Aug. 1976	13·2 ± 0·01	12·9–13·6	LL	1	4916	—	0·35	—	35–49
		Sept. 1977	15·3 ± 0·04	15·0–15·6	LL	1	458	—	12·01	—	28–32
		Sept. 1977	17·1 ± 0·07	16·4–17·9	10L:14D	1	328	—	3·35	—	25–26
		Sept. 1977	17·1 ± 0·05	16·5–17·4	10L:14D	2	206	135–276	13·73	11·85–15·60	23–29
		Aug. 1976	17·3 ± 0·03	16·1–17·7	LL	1	3786	—	1·08	—	25–29
	Seebach (stream)	May 1977	3·5 ± 0·03	2·5–4·8	10L:14D	1	2625	—	10·55	—	168–228
		May 1977	3·5 ± 0·03	2·5–4·8	10L:14D	1	—	—	—	—	178–204
		May 1977	4·6 ± 0·03	3·8–6·0	10L:14D	2	1468	1216–1756	5·37	0·99–9·74	114–136
		May 1977	4·6 ± 0·03	3·8–6·0	10L:14D	1	—	—	—	—	123–124
		May 1977	5·1 ± 0·05	2·4–7·8	DD	1	3576	—	11·13	—	98–112
		June 1977	5·2 ± 0·04	2·4–7·8	DD	1	2286	—	2·45	—	96–148
		May 1977	6·4 ± 0·01	6·0–7·0	10L:14D	3	1664	1036–2539	27·71	13·63–46·91	75–102
		June 1976	6·8 ± 0·09	5·5–8·4	DD	1	4230	—	35·82	—	72–86
		May 1977	7·9 ± 0·02	7·4–9·6	LL	1	1972	—	11·71	—	59–82
		June 1977	8·0 ± 0·03	7·6–9·6	LL	2	2345	1654–3036	28·83	3·51–54·15	55–67
		May 1977	9·9 ± 0·03	9·0–10·5	10L:14D	1	2426	—	6·50	—	35–43
		June 1976	10·1 ± 0·02	9·4–11·0	LL	2	3173	1809–4537	20·30	15·78–24·82	38–59
		May 1975	10·2 ± 0·04	9·8–10·3	LL	1	1882	—	3·40	—	41–52
		June 1975	10·3 ± 0·04	9·9–10·6	LL	1	1680	—	0·50	—	42–51
		April 1977	13·0 ± 0·01	12·6–13·3	10L:14D	3	3579	2542–4956	11·36	2·00–19·23	26–63
		June 1975	14·4 ± 0·04	14·2–14·9	LL	1	3657	—	14·40	—	21–38
		June 1977	15·0 ± 0·02	14·6–16·5	LL	1	2742	—	12·80	—	21–37
		May 1977	17·0 ± 0·03	16·3–17·7	10L:14D	1	3081	—	20·03	—	19–23
		May 1977	17·2 ± 0·05	16·2–18·1	10L:14D	2	1706	965–2446	1·37	1·35–1·39	18–22
		June 1977	19·8 ± 0·02	19·0–20·7	LL	1	2742	—	10·21	—	13–24
		June 1977	20·0 ± 0·03	19·6–20·5	LL	1	3030	—	17·69	—	14–29
		June 1977	20·4 ± 0·02	20·0–21·0	10L:14D	2	2875	2596–3154	39·89	25·11–54·66	11–30
		May 1977	8·2 ± 0·02	6·2–10·2	nLD (River)	1	—	—	—	—	—
E. torrentis	R. Lune	May 1978	3·9 ± 0·06	2·5–6·2	LL	3	750	631–834	22·58	9·19–32·28	200–350
		May 1978	8·8 ± 0·02	7·9–9·5	12L:12D	3	758	337–1184	29·11	21·96–35·94	46–62
		May 1978	11·4 ± 0·22	8·5–14·6	LL	3	858	511–1145	21·17	14·87–30·39	27–54
		May 1978	15·0 ± 0·05	14·0–15·7	12L:12D	4	998	443–1628	24·17	10·38–32·38	18–48
		May 1978	17·7 ± 0·09	16·8–18·5	LL	4	855	263–1157	23·22	13·69–31·49	12–24

		May 1978	19·5 ± 0·09	18·2–20·8	LL	4	955	389–1480	20·99	13·37–28·51	10–23
E. venosus	R. Brathay	May 1978	3·9 ± 0·06	2·5–6·2	LL	4	768	542–1178	23·28	2·84–46·44	210–310
		June 1978	8·7 ± 0·03	7·9–9·0	12L:12D	2	449	383–515	22·55	22·19–22·91	61–77
		May 1978	8·8 ± 0·02	7·9–9·5	12L:12D	1	353	—	68·56	—	53–70
		May 1978	11·4 ± 0·16	10·2–13·4	LL	1	806	—	21·09	—	30–40
		June 1978	14·5 ± 0·02	14·2–15·2	12L:12D	2	585	437–733	55·47	43·94–66·99	21–44
		May 1978	15·0 ± 0·05	14·5–15·7	12L:12D	2	714	629–799	40·41	18·15–62·64	21–32
		May 1978	17·8 ± 0·10	17·1–18·5	LL	2	945	800–1089	29·99	15·34–44·63	13–20
		May 1978	19·5 ± 0·09	17·0–21·1	LL	2	1124	1097–1151	31·27	14·49–48·05	12–17
		June 1978	19·9 ± 0·08	19·2–21·1	LL	2	462	420–503	52·77	45·53–60·00	11–20
	Seebach (stream)	June 1977	3·6 ± 0·03	2·5–5·2	10L:14D	1	825	—	4·49	—	280–350
		Sept. 1977	3·8 ± 0·05	2·5–5·2	10L:14D	1	129	—	24·81	—	245–270
		Sept. 1977	3·9 ± 0·06	2·5–5·2	10L:14D	1	83	—	7·23	—	275–315
		Sept. 1977	4·4 ± 0·03	3·9–4·8	10L:14D	2	409	108–709	13·50	12·04–14·95	190–265
		June 1977	4·5 ± 0·03	1·8–6·0	10L:14D	1	—	—	—	—	200–265
		June 1977	5·2 ± 0·01	4·5–6·1	LL	1	2830	—	4·35	—	140–190
		June 1977	8·1 ± 0·01	7·6–9·6	LL	1	3832	—	5·58	—	68–130
		Sept. 1977	8·1 ± 0·01	7·4–10·1	LL	2	170	121–218	4·91	6·61–3·21	76–110
		Sept. 1977	8·1 ± 0·01	7·4–10·1	LL	1	—	—	—	—	74–120
		July 1975	9·8 ± 0·03	9·4–10·6	LL	2	1192	1156–1228	3·39	0·43–6·35	50–66
		June 1977	10·1 ± 0·03	9·0–10·5	10L:14D	1	2530	—	14·20	—	49–70
		July 1976	10·1 ± 0·02	9·5–10·7	LL	2	2446	2346–2546	1·13	1·11–1·14	49–70
		Sept. 1977	10·2 ± 0·05	9·8–10·7	10L:14D	3	361	95–819	11·08	2·20–16·84	49–74
		June 1977	13·0 ± 0·03	12·6–13·4	10L:14D	1	2015	—	12·31	—	34–62
		Sept. 1977	13·2 ± 0·03	12·6–13·8	10L:14D	1	—	—	—	—	40–52
		Aug. 1976	13·3 ± 0·02	12·9–13·6	LL	1	735	—	7·07	—	32–42
		July 1975	15·1 ± 0·05	14·5–15·6	LL	2	887	733–1040	7·19	3·46–10·91	22–30
		Sept. 1976	15·1 ± 0·03	14·8–15·5	LL	1	1317	—	7·82	—	26–31
		June 1977	15·1 ± 0·02	14·7–16·5	LL	2	3044	1776–4312	3·65	0·68–6·61	26–44
		July 1976	15·2 ± 0·02	14·8–16·0	LL	1	2178	—	10·01	—	24–36
		June 1976	15·3 ± 0·02	15·0–15·6	LL	1	3571	—	1·15	—	25–31
		Sept. 1977	15·3 ± 0·01	15·0–15·6	LL	2	263	202–324	12·48	8·91–16·05	24–31
		Sept. 1977	15·3 ± 0·01	15·0–15·6	LL	1	—	—	—	—	27–34
		Sept. 1977	17·0 ± 0·05	16·4–17·4	10L:14D	2	125	104–145	17·55	4·80–30·30	23–36
		June 1977	17·2 ± 0·06	16·5–18·0	10L:14D	1	2243	—	42·44	—	18–42
		Sept. 1976	17·2 ± 0·03	16·1–17·6	LL	1	1067	—	2·06	—	27–32
		Aug. 1976	17·3 ± 0·05	16·2–17·8	LL	1	891	—	3·93	—	19–32
		June 1977	19·8 ± 0·02	19·0–20·7	LL	2	2047	1839–2254	27·85	10·50–45·20	13–29
		Aug. 1977	20·4 ± 0·04	19·9–21·2	LL	2	211	54–368	13·35	9·30–17·4	15–21
		Aug. 1977	20·4 ± 0·04	19·9–21·2	LL	1	—	—	—	—	14–22
		Sept. 1977	20·6 ± 0·03	20·3–21·0	10L:14D	2	136	69–203	6·30	5·40–7·20	16–25
		Aug. 1972	*c.* 10·0	—	LL	1	—	—	—	—	52–56
		Aug. 1972	*c.* 15·0	—	LL	1	—	—	—	—	25–32
		Aug. 1972	*c.* 20·0	—	LL	1	—	—	—	—	14–20